Research

Ecography 30: 483–490, 2007
doi: 10.1111/j.2007.0906-7590.05072.x

Subject Editor: Kevin Burns. Accepted 11 June 2007

Crop seed spillage along roads: a factor of uncertainty in the containment of GMO

Moritz von der Lippe and Ingo Kowarik

M. von der Lippe (moritz.vdlippe@tu-berlin.de) and Ingo Kowarik, Inst. of Ecology, Technical Univ. of Berlin, Rothenburgstr.12, DE-12165 Berlin, Germany.

Feral populations of crop species along roadsides contribute to the uncertainty regarding the containment of genetically modified (GM) crops, as the feral populations could promote the persistence of transgenes outside of cultivated fields. Roadside populations of several common crop species are known to occur far from arable fields, and the dispersal pathways that promote their recruitment in road verges are unclear. Human-aided dispersal, in particular adhesive dispersal by vehicles, has been suggested as a possible vector, but this has not yet been proven experimentally. We sampled the seed rain from vehicles inside two motorway tunnels in an urban environment to reveal the contribution of crop species to seeds unintentionally dispersed by traffic beyond agricultural production areas. Three species of arable crops, wheat *Triticum aestivum*, rye *Secale cereale* and oilseed rape *Brassica napus*, were among the most frequent species deposited by vehicles inside the motorway tunnels. Each of the three species was clearly more predominant in one direction of traffic. While seeds of *Triticum aestivum* and *Secale cereale* were primarily transported into the city, *Brassica napus* was significantly more abundant in samples from lanes leading out of the city. Seed sources in the local surroundings of the tunnels were virtually nonexistent, and the high magnitude of seed deposition combined with high seed weights suggests a dispersal mechanism different from other species in the sample, at least for *Triticum aestivum* and *Secale cereale*. This provides evidence that spillage during transport is a major driver for long-distance dispersal of crops. Our results suggest that seed dispersal by vehicles is the major driver in the recruitment of roadside populations of arable crops, providing a possible escape route for GM crops. Risk management should thus aim at curbing transport losses of GM crops.

Roadsides and urban areas are important habitats for feral populations of some common arable crop species, such as *Brassica napus*, *Triticum aestivum* and *Secale cereale* (Burton 1983, Brandes and Griese 1991, Langer 1994, Crawley and Brown 1995, Landolt 2001, Pessel et al. 2001, Adler and Mrkvicka 2003). As these populations are usually transient (Burton 1983, Landolt 2001, Crawley and Brown 2004), it is striking that numerous sites along roads and urban areas are occupied by feral crops even far from arable fields. This phenomenon has primarily been studied in *Brassica napus* as feral populations of this species are markedly clumped along roadsides. Roadside populations of *Brassica napus* show high population dynamics including high rates of colonisation of new sites and a high probability of local extinction (Pessel et al. 2001, Crawley and Brown 2004, Claessen et al. 2005).

The occurrence of feral crop populations far from arable fields as well as their population dynamics suggest that most roadside populations rely on repeated introductions of seeds due to human-mediated long-distance dispersal. However, the actual dispersal pathways and escape routes remain unknown.

Seed dispersal by vehicles from feral roadside populations has been suggested as a relevant mechanism for the colonisation of new sites by *Brassica napus* in urban areas (Breckling and Menzel 2004). Pessel et al. (2001) showed that cultivars of *Brassica napus* that had long been unavailable on the market persisted for at least 8 yr in the roadside vegetation. The authors suggested that seed sources other than spillage or adjacent arable fields contribute to the dynamics of feral *Brassica napus* populations. In contrast, Crawley and Brown (2004) found higher abundances of *Brassica napus* in road verges of lanes leading to an oilseed processing plant compared to the opposite verge and therefore assumed that seeds spilled from lorries were the main source for the new populations.

As the role of vehicles as dispersal vectors of arable crops has not yet been investigated experimentally, uncertainty exists about the relevance of this pathway for the further spread of genetically modified (GM) crops. Containment of GM crops is an important objective for avoiding gene flow from GM organisms (GMO) to wild relatives and for separating conventional farming from farming with GM crops.

Possible escape routes from cultivation for GMO are pollen dispersal and seed dispersal. Most approaches for risk assessment of GM crops focus on pollen dispersal, as this mechanism exerts the most immediate effects on gene flow from crops to wild relatives (Dale et al. 2002, Thompson et al. 2003, Pilson and Prendeville 2004, Walklate et al. 2004, Firbank et al. 2005). Gene flow between crops and wild relatives, including the escape of transgenes into wild populations, by pollen dispersal has been demonstrated for several species (Dale et al. 2002, Beckie et al. 2003, Hegde and Waines 2004, Pilson and Prendeville 2004, Walklate et al. 2004, Devaux et al. 2005, Gustafson et al. 2005). Although pollen dispersal in crop species usually declines sharply within a few hundred metres of the pollen source, several studies report a notable number of pollination events >1 km from the pollen source (Squire et al. 1999, Devaux et al. 2005).

The spatial effectiveness of seed dispersal is usually much lower compared to pollen dispersal if standard means (i.e. self-dispersal, wind-dispersal) are considered, since most crop species show no natural adaptation for long-distance seed dispersal. However, a high potential for human-mediated long-distance dispersal exists in cropping systems, as seeds of crops or co-occurring weeds can be dispersed by agricultural engines (Mayer 2000), during harvesting (Price et al. 1996) and by spillage from harvest transports (Crawley and Brown 2004). Seed dispersal has important implications for gene flow between GM crops and wild relatives or conventional crops by 1) decreasing the distance between GM crops and populations of their wild relatives or overcoming spatial isolation between GMO and conventional arable fields and 2) establishing self-sustaining feral crop populations outside of cultivated fields that increase the chance of gene flow in space and time.

Furthermore, there is evidence that seed dispersal supports the escape of weedy lineages from fields. Feral populations of *Beta vulgaris* outside cultivated fields of French sugar beet are known to have descended from cultivated maternal ancestors (Arnaud et al. 2003, Sukopp et al. 2005). This suggests that seed dispersal of cultivated crops contributes to the occurrence of hybrids outside arable fields.

The presence of feral crop populations outside of cultivated fields increases the potential for subsequent gene flow to wild relatives. Furthermore, it makes containment more uncertain as little is known about the distribution of feral populations (Gressel 2005), and control is much more difficult than with volunteer crops in arable fields. Because dispersal rates and the mean distance of dispersal events greatly influence growth rates and persistence of populations (Claessen et al. 2005, Garnier and Lecomte 2006), anthropogenic long-distance dispersal is likely to increase the spread of feral *Brassica napus* and potentially also of other crops. Knowledge about the underlying mechanisms that lead to the establishment of feral crop populations outside of cultivated fields is thus a crucial prerequisite for successful risk management (Breckling and Menzel 2004).

These findings stress the need for specific knowledge of the actual dispersal pathways that lead to the escape of arable crops from cultivation. Transport of seeds by vehicles has been acknowledged as an efficient dispersal vector of plant species (Hodkinson and Thompson 1997, Zwaenepoel et al. 2006, Kowarik and von der Lippe 2007) but has not yet been shown to be relevant for crop species. A companion study revealed that a large share of plant species that are dispersed by vehicles were moved over long distances, and that this mechanism especially favours the dispersal of non-native species (von der Lippe and Kowarik 2007).

This study attempts to estimate the role that seed deposition by vehicles plays in the dynamics of feral crop populations along road verges and to determine the main dispersal pathways behind this phenomenon.

By measuring the deposition of seeds along the roadsides in two motorway tunnels, we address the following questions: 1) to what extent are seeds of arable crops deposited by vehicles along roadsides? 2) If there is a relevant deposition of seeds, are the likely potential seed sources transport losses, adjacent arable fields or feral roadside populations? 3) How is the rate of seed deposition related to traffic direction or location of carriageways?

Material and methods

Study sites and sampling design

We used two long motorway tunnels in Berlin, Germany, as sampling sites to isolate vehicles from other seed dispersal vectors. The tunnels were located

2 km apart along the same motorway, leading from the inner city to the northwest outskirts of Berlin. The first tunnel was near the inner city ("urban tunnel") in a dense residential area, the second ("suburban tunnel") was located in a low-density residential area with a high proportion of urban wasteland and railroad areas in the surroundings. Inbound and outbound traffic in each tunnel was divided by a continuous solid wall, providing independent samples for both directions of the motorway.

Special seed traps were constructed to provide a large sampling surface close to the ground. Each trap consisted of a flat, 1.9-m-long container ($1.9 \times 0.08 \times 0.05$ m) made of sheet metal and a removable aluminium funnel for protection from airflow (von der Lippe and Kowarik 2007). The funnel provided a sampling surface of 0.22 m^2. The traps were installed parallel to the motorway ca 1 m from the gutter to collect the seed rain at the road verges. Beginning 150 m from the tunnel entrances, five traps were placed in each direction, spaced 2 m apart, providing a total of 20 replicates at each sampling date.

In a 1-yr sampling period between 30 October, 2002, and 29 October, 2003, we sampled all 20 seed traps six times. As access to the tunnels was limited to the regular dates of street cleaning, the exposure periods varied as shown in Table 1. The routine cleaning of the tunnels before each sampling period began ensured that the collected samples mostly reflected the actual seed deposition caused by traffic during each sampling period.

Glasshouse germination of seeds

For species determination, seeds of each sample gathered from the seed traps were germinated in a glasshouse according to Ter Heerdt et al. (1996). To standardise germination conditions, all samples were kept for 6 weeks in an unlighted climate chamber at 3–5°C for cold stratification. Samples were concentrated by wet sieving with a 0.2-mm-mesh sieve and spread thinly (<0.5 cm) over sterilised potting soil in germination trays (32×50 cm). Every sample was kept in a temperature-controlled (min. 15°C; max. 30°C) glasshouse for 12 months after sowing. Trays were watered when necessary to keep the soil surface moist. After species identification, seedlings were removed from the germination trays. Only seedlings of species that could not be identified were potted and grown until identification was possible. Nomenclature followed Wisskirchen and Haeupler (1998).

Germination trays were positioned on tables that were enclosed by a tent of garden fleece to avoid influx of wind-borne seeds. At the same time, three to five trays (ca 10% of the total trays) were filled with pure sterilised potting substrate to control for possible impacts of wind-dispersed seeds and any remaining viable seeds in the potting mixture. Five species germinated sparsely in the control trays towards the end of the germination periods and were omitted from the whole dataset.

Table 1. Exposure periods and sampling dates for seed sampling from 20 seed traps installed in two motorway tunnels.

Exposure periods of seed traps (sampling dates in bold)	Days of exposure
30.10.2002–**11.03.2003**	133
12.03.2003–**17.06.2003**	98
18.06.2003–**22.07.2003**	35
23.07.2003–**03.09.2003**	43
04.09.2003–**06.10.2003**	33
07.10.2003–**29.10.2003**	23

Inventories of the adjacent flora and of feral roadside crops

To assess the potential impact of adjacent seed sources on the seed deposition in the tunnels, we surveyed the flora within a radius of 100 m around the tunnel entrances between 5 and 15 May, 2003, and again between 20 July and 2 August, 2003. In addition, feral crop populations in the road verges of the motorway within at least 2 km of every tunnel entrance were mapped.

Statistical analysis

Crop species represented by >100 seeds in the total sample were chosen for further analysis. To test for significant effects of the tunnel location (urban vs suburban) and direction of traffic flow (outbound vs inbound) on the magnitude of seed deposition, we conducted a two-way ANOVA with tunnel and traffic direction as explanatory variables and counts of emerged seedlings of the chosen species as dependent variables. Seed counts were square-root transformed to meet the assumption of normality.

To reveal if the deposition of seeds of arable crops is likely to result from the same means of dispersal as the other species in the sample, we plotted their mean seed weights against their abundance in the samples. Low seed weight has been shown to be a relevant factor in adhesion to vehicles (Hodkinson and Thompson 1997, Zwaenepoel et al. 2006), and large deviance of crop species from the mean seed weight of other species in the samples could indicate a different transport mechanism, especially when combined with unusually high seed counts. Only species with more than one occurrence in the samples were included in the analysis.

We used data on seed weights from Otto (2002) that were available for most species in the seed samples.

All statistical analysis was carried out in SPSS, ver. 13.

Results

Magnitude and seasonal variation in seed deposition

Vehicles unintentionally released sizeable amounts of arable crop seeds along the roadsides in the tunnels. Altogether, seedlings of five species of arable crops germinated from the samples from inside the two motorway tunnels (Table 2), comprising 3.0% of the 168 total species in the samples. The quantitative extent of seed deposition of arable crops by vehicles was even greater than would be expected from the species share. Nearly every fourth seedling (25.1%) that emerged from the tunnel samples was an arable crop.

Three arable crop species were frequently encountered. *Triticum aestivum* was the most frequent of all species with 900 seedlings emerging from the samples (Table 2). *Secale cereale* (190 seeds) and *Brassica napus* (121 seeds) were second and third among the arable crops. Taken together, these three species constituted 24.8% of the total number of viable seeds trapped and 98.1% of all arable crop seeds. The remaining arable crops, *Hordeum vulgare* (9 seeds) and *Avena sativa* (4 seeds), reached seed numbers that were about one order of magnitude lower than the three most frequent species. *Triticum aestivum*, *Secale cereale* and *Brassica napus* were chosen for further investigation as they occurred in sufficient frequencies for statistical analysis.

Table 2. The most abundant plant species in seed samples of 20 seed traps gathered in two motorway tunnels in Berlin, Germany, over a 1-yr sampling period. Agricultural crops are in bold. The other two crop species that were found in the samples are also displayed with their seed numbers and their abundance rank.

Rank	Species	Seed#
1	***Triticum aestivum***	**900**
2	*Sagina procumbens*	387
3	*Poa annua*	322
4	*Plantago major*	240
5	***Secale cereale***	**190**
6	*Conyza canadensis*	187
7	*Chenopodium album*	169
8	***Brassica napus***	**121**
9	*Lepidium ruderale*	117
10	*Polygonum aviculare agg.*	106
52	***Hordeum vulgare***	**9**
71	***Avena sativa***	**4**

The mean annual seed rain of arable crops in the four tunnel lanes ranged from 13.0 to 124.0 seeds per trap (59–564 seeds m^{-2} yr^{-1}) for all crops: from 8.8 to 97.8 seeds per trap (40–445 seeds m^{-2} yr^{-1}) for *Triticum aestivum*, from 0.2 to 21.2 seeds per trap (1–96 seeds m^{-2} yr^{-1}) for *Secale cereale* and from 0.4 to 14.4 seeds per trap (2–67 seeds m^{-2} yr^{-1}) for *Brassica napus* (Fig. 1).

There was a high seasonal variation in seed deposition among the most frequent crop species (Fig. 2). Seeds of *Brassica napus* and *Secale cereale* were deposited for a period of ca 4 months, with a later deposition in the latter species. In contrast, *Triticum aestivum* was deposited over the complete sampling period.

Spatial variation in seed deposition

The most frequent crop species showed a clear association with a specific direction of traffic flow (Fig. 1). Seedlings of *Brassica napus* emerged significantly more frequently from outbound than from inbound samples, while the opposite was found for *Triticum aestivum* and *Secale cereale* (Table 3).

Brassica napus and *Triticum aestivum* occurred significantly more frequently in the suburban tunnel than in the urban tunnel, while the tunnel location had no significant effect on the number of *Secale cereale* seeds (Table 3). A significant interaction between tunnel location and traffic direction occurred only for *Triticum aestivum*, with the two effects influencing the rate of seed deposition to different extents (Table 3).

Relation between seed weight and abundance in the samples

The seed weight of the three most common arable crop species was rather high compared to all other species in the samples (Fig. 3a). While all other species appear to be restricted to either low abundance in the sample or low seed weight, the three arable crop species combine high abundance and high seed weight. This picture becomes even clearer if only those species with no potential seed sources in the direct vicinity of the tunnels are compared (Fig. 3b). In this case, each of the three most frequent arable crops accounts for more than twice as many seeds in the samples as the most abundant non-crop species. They are thus the only species that fall above the 95% percentile of the seed counts. At the same time, *Triticum aestivum* and *Secale cereale* also fall above the 95% percentile of the seed weight values.

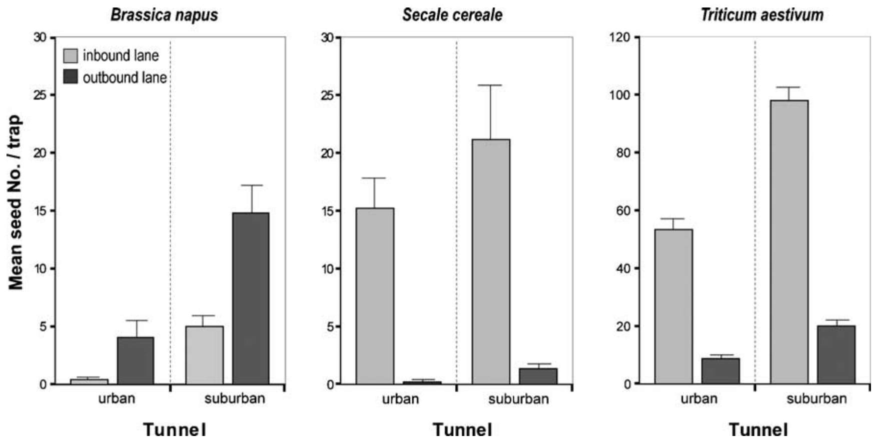

Fig. 1. Mean annual seed deposition per seed trap by vehicles in both directions of two motorway tunnels for three arable crops (n = 5 per lane). Error bars show 1 SE. Note the different scale on the y-axis for *Triticum aestivum*.

Potential seed sources

None of the three species occurred in the immediate surroundings (< 100 m) of the tunnel entrances except for two single plants of *Triticum aestivum* around the entrances of the urban inbound lane and the suburban outbound lane. No roadside populations of the crop species occurred within 1 km of the tunnels, and no arable fields were located within at least 3 km of either tunnel. There was a sizeable roadside population of *Brassica napus* along both motorway verges beyond the city borders, but only at a distance of > 1 km from the suburban tunnel.

Discussion

An unexpectedly high number of seedlings of arable crops emerged from the tunnel samples. *Triticum aestivum* was the most frequent species, and its seed deposition exceeded that of species with very light or wind-dispersed seeds such as *Sagina procumbens* or *Conyza canadensis*. A corresponding magnitude of seed deposition of crop species outside of arable fields has, to our knowledge, not yet been reported elsewhere.

Seed releases on arable fields up to two orders of magnitude higher than those we observed along roadsides have been reported (Price et al. 1996, Pekrun et al. 1998). Mean annual seed depositions up to 67 and 445 seeds m^{-2} yr^{-1} for *Brassica napus* and *Triticum aestivum,* respectively, however, indicate a reliable likelihood that traffic-mediated dispersal can enhance establishment in suitable roadside habitats. Along roads that are not subject to frequent mowing or herbicide spraying, some crop species could have a better chance of establishment than volunteers in fields where young seedlings could be disturbed by delayed tillage. Previous studies on vehicle-mediated seed transport (Hodkinson and Thompson 1997, Zwaenepoel et al. 2006) did not find any of the crop species we found in our study although one of them took place in a rural area (Schmidt 1989). This may be due to methodological restrictions of studies that identify car-borne flora by analyzing mud attached to vehicles. Since our approach

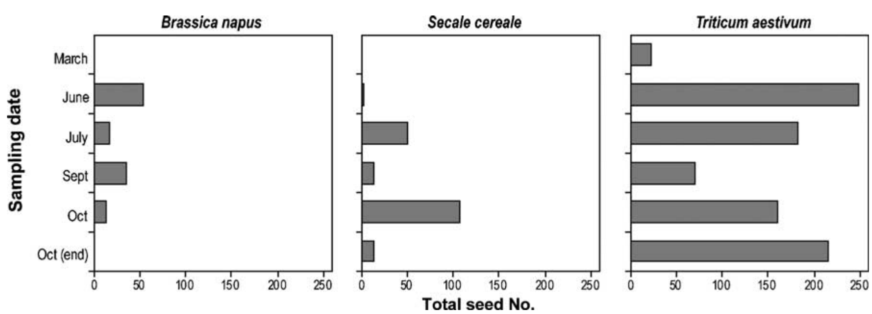

Fig. 2. Seasonal variation in the total viable seed deposition by vehicles in 20 seed traps inside two motorway tunnels for three arable crops.

Table 3. ANOVA results for effects of direction of traffic flow (into the city vs out of the city) and tunnel location (urban vs suburban tunnel) on seed counts of three arable crops deposited in the tunnel samples. Seed counts were square-root transformed.

	Brassica napus		*Triticum aestivum*		*Secale cereale*		df
	F	p	F	p	F	p	
Direction	19.16	<0.001	467.48	<0.001	77.56	<0.001	16
Tunnel	33.74	<0.001	84.30	<0.001	3.26	0.090	16
Tunnel × direction	0.17	0.687	5.71	0.030	0.11	0.749	16

allows us to measure the seed deposition directly along roads, our samples include seeds that were transported by adhesion to vehicles via mud as well as seeds that move on the loading area and may be dispersed by spillage.

Several pieces of evidence point to seeds spilled from lorries as a major origin of the high seed deposition of arable crops along the roadsides: 1) seasonal variation in seed deposition (Fig. 2) does not match the species' periods of seed release. 2) Feral crop populations providing potential seed sources are virtually absent in the surroundings of the tunnels as well as along the entire motorway transect. 3) The exceptionally high rate of seed deposition combined with high seed weight suggests a dispersal pathway that is different from other species in the sample which were presumably transported through attachment to vehicles by mud (von der Lippe and Kowarik 2007).

These criteria apply to *Triticum aestivum* especially, as this species was observed during the entire sampling period and was the most frequent species with the heaviest seeds of all species in the sample. *Secale cereale* was deposited for a shorter period (Fig. 2), but the first peak of deposition in July clearly precedes the time of seed release from arable fields or feral populations.

For *Brassica napus*, the picture is not as clear, as this species was less abundant in the samples and has much lighter seeds. However, two main points suggest transport losses by spillage as an important pathway of dispersal for this species as well. Firstly, the peak of rapeseed deposition in the 17 June sample is quite unlikely to result from early seed release of feral populations and subsequent transport by attachment to vehicles. *Brassica napus* normally reaches seed maturity at the beginning of August, and although early seed releases in feral populations have been observed as early as mid-June (Haeupler et al. 2004), the major seed shadow from the feral population could not be expected to take place in the first half of June.

Secondly, the observed association of the main seed deposition with the outbound lane does not relate to the closest roadside populations of *Brassica napus*, which were located at a distance of >1 km from the tunnel entrance outside of the city. No urban roadside populations that might function as source for the seeds recorded in the outbound lane were found within 1 km from the tunnel entrances. For both *Brassica napus* and *Triticum aestivum*, the higher seed deposition in the suburban tunnel (Table 3) indicates that urban feral populations do not act as significant seed sources,

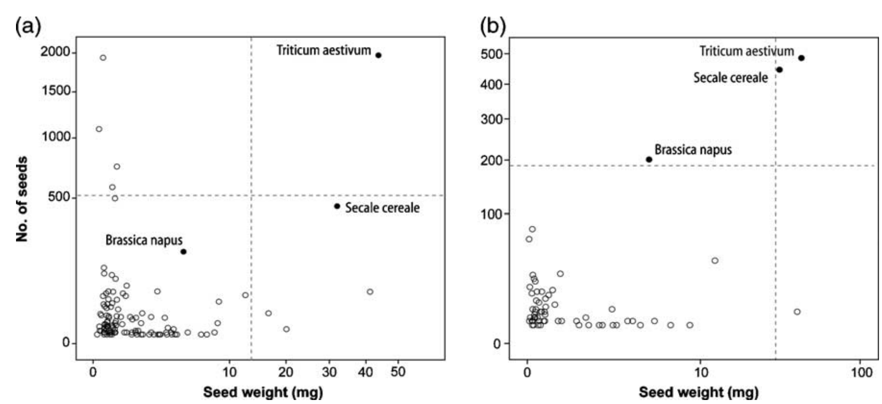

Fig. 3. Counts of viable seeds of different species in the total tunnel sample plotted against their mean seed weight (seed weight data taken from Otto 2002). (a) All seeds with more than one occurrence in the sample (n = 113). (b) Only seeds of species absent from within 100 m of the tunnel entrances and with more than one occurrence in the samples (n = 61). *Brassica napus*, *Triticum aestivum* and *Secale cereale* are highlighted by filled circles. The dotted lines show the 95% percentiles of both variables. The x-axis is log-scaled, the y-axis is square-root scaled.

although feral populations of *Brassica napus* in the urban area of Berlin (B. Seitz pers. comm. from the Berlin floristic mapping) may function as additional seed sources.

Crawley and Brown (2004) found different densities of *Brassica napus* on opposite verges of a motorway. Our results confirm that such differences can in fact reflect different patterns of seed deposition by vehicles (Fig. 1). As several motorway entrances exist between the urban and the suburban tunnels, we hypothesize that the variation in crop seed deposition among tunnels mainly results from differing uses of single sections of the motorway by lorries carrying crop seeds.

As standard agricultural transport vehicles with a minimum speed of <60 km h^{-1} have no access to motorways, the seed deposition of crops in the tunnels can not be due to farm vehicles transporting harvests from arable fields. Thus, secondary harvest transports from silos to processing plants are likely primary sources of seed spillage. This is striking for *Brassica napus* because rape is usually transported in closed-tank lorries (Breckling et al. 2003). An alternative explanation for the high seed deposition of crops along roadsides could be spillage of forage from cattle transports.

Implications for the containment of GM crops

Our results suggest that traffic-mediated long-distance dispersal of seeds provides an extensive route of escape for arable crops from cultivation. It probably accounts for the majority of roadside populations of the species involved, although for *Brassica napus* in particular, subsequent dispersal from feral populations might be a secondary pathway. The fact that this seed deposition was measured in an urban area, far from agricultural production areas, demonstrates the outstanding spatial effectiveness of vehicles as vectors for the unintentional transfer of crop seeds. Hence, to avoid seed dispersal outside of cultivated land, risk management for GM crops should include the thus-far-neglected transportation sector. Transport of harvest in closed-tank lorries is probably appropriate but should be checked for efficient containment of seeds. Further studies should elucidate if spillage from cattle transports is a relevant dispersal vector.

Acknowledgements – This study was supported by the postgraduate research and study program (DFG – GRK 780) Perspectives on Urban Ecology – the Example of the European Metropolis of Berlin. We thank T. Bachmann and Y. Golopasany for technical assistance and K. Vargas for improving the English. K. C. Burns, U. Sukopp and H. Jäger provided helpful comments on earlier drafts of this paper.

References

Adler, W. and Mrkvicka, A. C. 2003. Die Flora Wiens, gestern und heute. – Verlag des Naturhistorischen Museums Wien.

Arnaud, J. F. et al. 2003. Evidence for gene flow via seed dispersal from crop to wild relatives in *Beta vulgaris* (Chenopodiaceae): consequences for the release of genetically modified crop species with weedy lineages. – Proc. R. Soc. B 270: 1565–1571.

Beckie, H. J. et al. 2003. Gene flow in commercial fields of herbicide-resistant canola (*Brassica napus*). – Ecol. Appl. 13: 1276–1294.

Brandes, D. and Griese, D. 1991. Siedlungs- und Ruderalvegetation von Niedersachsen. Eine kritische Übersicht. – Universitätsbibliothek der TU Braunschweig.

Breckling, B. and Menzel, G. 2004. Self-organised pattern in oilseed rape distribution – an issue to be considered in risk analysis. – In: Breckling, B. and Verhoeven, R. (eds), Risk hazard damage – specification of criteria to assess environmental impact of genetically modified organisms. Landwirtschaftsverlag, pp. 73–88.

Breckling, B. et al. 2003. Biologische Risikoforschung zu gentechnisch veränderten Pflanzen in der Landwirtschaft: Das Beispiel Raps in Norddeutschland. – In: Reuter, H. et al. (eds), Gene, Bits und Ökosysteme. P. Lang Verlag, pp. 19–45.

Burton, R. M. 1983. Flora of the London area. – London Natural History Society.

Claessen, D. et al. 2005. Which traits promote persistence of feral GM crops? Part 2: implications of metapopulation structure. – Oikos 110: 30–42.

Crawley, M. J. and Brown, S. L. 1995. Seed limitation and the dynamics of feral oilseed rape on the M25 motorway. – Proc. R. Soc. B 259: 49–54.

Crawley, M. J. and Brown, S. L. 2004. Spatially structured population dynamics in feral oilseed rape. – Proc. R. Soc. B 271: 1909–1916.

Dale, P. J. et al. 2002. Potential for the environmental impact of transgenic crops. – Nat. Biotechnol. 20: 567–574.

Devaux, C. et al. 2005. High diversity of oilseed rape pollen clouds over an agro-ecosystem indicates long-distance dispersal. – Mol. Ecol. 14: 2269–2280.

Firbank, L. et al. 2005. Reassessing the environmental risks of GM crops. – Nat. Biotechnol. 23: 1475–1476.

Garnier, A. and Lecomte, J. 2006. Using a spatial and stage-structured invasion model to assess the spread of feral populations of transgenic oilseed rape. – Ecol. Modell. 194: 141–149.

Gressel, J. 2005. Introduction – the challenges of ferality. – In: Gressel, J. (ed.), Crop ferality and volunteerism. CRC Press, pp. 45–57.

Gustafson, D. I. et al. 2005. An empirical model for pollen-mediated gene flow in wheat. – Crop Sci. 45: 1286–1294.

Haeupler, H. et al. 2004. Geobotanische Untersuchungen zum Vergleich von gentechnisch verändertem und "konventionellem" Raps. – Floristische Rundbriefe Beih. 7: 3–109.
Hegde, S. G. and Waines, J. G. 2004. Hybridization and introgression between bread wheat and wild and weedy relatives in North America. – Crop Sci. 44: 1145–1155.
Hodkinson, D. J. and Thompson, K. 1997. Plant dispersal: the role of man. – J. Appl. Ecol. 34: 1484–1496.
Kowarik, I. and von der Lippe, M. 2007. Pathways in plant invasions. – In: Nentwig, W. (ed.), Biological invasions. Ecol. Stud. 193, Springer, pp. 29–47.
Landolt, E. 2001. Flora der Stadt Zürich. – Birkhäuser Verlag.
Langer, A. 1994. Flora und Vegetation städtischer Straßen am Beispiel Berlin. – Technische Univ. Berlin.
Mayer, F. 2000. Long distance dispersal of weed diaspores in agricultural landscapes – the Scheyern approach. – Shaker.
Otto, B. 2002. Merkmale von Samen, Früchten, generativen Germinulen und generativen Diasporen. – In: Klotz, S. et al. (eds), BIOLFLOR – Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland Bundesamt für Naturschutz, pp. 177–196.
Pekrun, C. et al. 1998. Cultural control of volunteer oilseed rape (*Brassica napus*). – J. Agricult. Sci. 130: 155–163.
Pessel, F. D. et al. 2001. Persistence of oilseed rape (*Brassica napus* L.) outside of cultivated fields. – Theor. Appl. Gen. 102: 841–846.
Pilson, D. and Prendeville, H. R. 2004. Ecological effects of transgenic crops and the escape of transgenes into wild populations. – Annu. Rev. Ecol. Evol. Syst. 35: 149–174.
Price, J. S. et al. 1996. Seed losses in commercial harvesting of oilseed rape. – J. Agricult. Engin. Res. 65: 183–191.
Schmidt, W. 1989. Plant dispersal by motor cars. – Vegetatio 70: 147–152.
Squire, G. R. et al. 1999. Gene flow at the landscape level. – In: Lutman, P. J. W. (ed.), Gene flow and agriculture: relevance for transgenic crops. British Crop Protection Council, pp. 57–64.
Sukopp, U. et al. 2005. Feral beets – with help from the maritime wild? – In: Gressel, J. (ed.), Crop ferality and volunteerism. CRC Press, pp. 45–57.
Ter Heerdt, G. N. J. et al. 1996. An improved method for seed bank analysis: seedling emergence after removing the soil by sieving. – Funct. Ecol. 10: 144–151.
Thompson, C. J. et al. 2003. Model-based analysis of the likelihood of gene introgression from genetically modified crops into wild relatives. – Ecol. Modell. 162: 199–209.
von der Lippe, M. and Kowarik, I. 2007. Long-distance dispersal of plants by vehicles as driver in plant invasions. – Conserv. Biol. 21: 986–996.
Walklate, P. J. et al. 2004. A model of pollen-mediated gene flow for oilseed rape. – Proc. R. Soc. B 271: 441–449.
Wisskirchen, R. and Haeupler, H. 1998. Standardliste der Farn- und Blütenpflanzen Deutschlands. – Ulmer.
Zwaenepoel, A. et al. 2006. Motor vehicles as vectors of plant species from road verges in a suburban environment. – Basic Appl. Ecol. 7: 83–95.